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Progress in Oceanography 60 (2004) 143–164
Progress in Oceanography
www.elsevier.com/locate/pocean

Detecting regime shifts in the ocean: data considerations

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Abstract

We review observational data sets that have been used to detect regime shifts in the ocean. Through exploration of data time series we develop a definition of a regime shift from a pragmatic perspective, in which a shift is considered as an abrupt change from a quantifiable ecosystem state. We conclude that such changes represent a restructuring of the ecosystem state in some substantial sense that persists for long enough that a new quasi-equilibrium state can be observed. The abruptness of the shift is relative to the life-scale or the reproductive time-scale of the higher predators that are influenced by the shift. In general, the event-forcing is external to the biological ecosystem, usually the physical climate system, but we also identify shifts that can be ascribed to anthropogenic forcing, in our examples fishing. This pragmatic definition allows for several different types of regime shift ranging from simple biogeographic shifts to non-linear state changes. In practice it is quite difficult to determine whether observed changes in an oceanic ecosystem are primarily spatial or temporally regulated. The determination of ecosystem state remains an unresolved, and imprecise, oceanographic problem.

We review observations and interpretation from several different oceanic regions as examples to illustrate this pragmatic definition of a regime shift: the Northeast Pacific, the Northwest and Northeast Atlantic, and Eastern Boundary Currents. For each region, different types of data (biological and physical) are available for differing periods of time, and we conclude, with varying degrees of certainty, whether a regime shift is in fact detectable in the data.

Contents

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doi:10.1016/j.pocean.2004.02.017

1. Introduction

The concept of regime shifts in marine ecosystems has gained currency over the past several decades with perhaps the most enthusiasm for the concept having developed in the North Pacific where there have been many publications (for example, Polovina, Mitchum, & Evans, 1995; Ware, 1995; Francis, Hare, Hollowed, & Wooster, 1998; Hare & Mantua, 2000). While conceptually straightforward, understanding and identifying a regime shift concept has proven difficult. If we can define an ecosystem state, then it seems clear that a change in state, in the dynamical sense, should be measurable and that some such changes in state can be substantial, abrupt and persistent. The implementation of this simple definition in marine ecosystems has proven difficult, although there has been substantial progress in understanding the functional and dynamical meaning of the concept in freshwater systems (cf. Sheffer, Carpenter, Foley, Folkes, & Walker, 2001). Closed freshwater/lake systems have been studied to a degree that is typically not possible for very large and open marine (eco)systems, yet it seems likely that well-documented and understood state shifts in lake systems will offer important insights into marine regime shifts (Sheffer et al., 2001; Scheffer & van Nes, 2004). In our analysis, we take a pragmatic perspective, rather than a theoretical one, and focus primarily upon the data themselves. Not worrying too much about the dynamical perspective, we consider how regime shifts can be identified from marine ecosystem data and what characteristics can be used as reference points for regime shifts in the ocean. There are clear implications for this pragmatic approach, and we will explore them through the regional analysis (Pacific, Atlantic and Boundary Currents) that we present.

One reason for the developing interest in regime shifts in the ocean is that some ocean time series (plankton, fish, temperature) are approaching, or now exceed, 50 years in length, for example the Continuous Plankton Recorder survey (Warner & Hays, 1994) and the CalCOFI survey (Rebstock, 2002) and it is now possible to see interannual and decadal variability that has been difficult, or impossible, to resolve in shorter time series. Time series spanning all levels of the ecosystem, from nutrients through phytoplankton and zooplankton to fish and birds and mammals are still rare, and for the most part shorter than 50 years in length, but there are now also proxy time series of biological (Baumgartner, Soutar, & Ferriera-Bartina, 1992; Satterfield & Finney, 2002) and physical data proxies (Marshall et al., 2001) that allow us to extend our analysis back hundreds of years. Some of these time series have revealed interannual and interdecadal correlations between the physical and biological environment that can at times be quite abrupt. What are the conditions for such changes that should be considered as regime shifts?

The concept of a regime shift is more easily definable and accepted in the physical modeling community (Rahmstorf, 1999). On very long time scales, tens of thousands of years, it appears that the Vostock ice core signal indicates that the earth moves between two relatively stable states of warm and cold conditions (Petit et al., 1999). At millennial time-scales, there also appear to be alternate stable states in the earth system, with the thermohaline circulation of the ocean playing a key role (Alley et al., 2003). There is thus some general acceptance in the earth sciences community that the ocean/atmosphere system can move abruptly between equilibrium states, at least on climatic time-scales. The primary interannual and interdecadal patterns of variability (the El Niño-Southern Oscillation or ENSO, the Pacific Decadal Oscillation PDO, the North Atlantic Oscillation NAO and others.) have not so far been considered as moving between different regimes but instead relatively smooth and continuous 'oscillations'. In some cases (e.g., the NAO) there is little evidence for anything like a regular periodicity, while for the ENSO phenomenon it is clear that the dominant time-scale of variability is from about 2 to 7 years (Rasmussen & Carpenter, 1982). In the Pacific, interdecadal variability that has been associated with marine ecosystem regime shifts is pronounced at periods of ~15-to-25 and ~50-to-70 years (Minobe, 1999), though the statistical significance of these periods is weak as they are derived from century long climate records (e.g., Wunsch, 1999; Rudnick & Davis, 2003).

The key characteristic of a regime shift is that the time-scale for the change between states is much shorter than the time within alternate states. This pragmatic definition can be applied, or perhaps tested, by measuring the rate of change of the time series. The description of the state itself cannot of necessity be precise, as we have not yet developed a very tight definition of ecosystem state (e.g., see Longhurst, 1998). The differences between states should include more than just a few components of the ecosystem and cover more than one trophic level and more than a single species. We are looking for substantial changes in ecosystem structure such that key, or important, pathways of energy flow or distribution are altered. The time-scale for the change is expected to be less than that of the longer-lived species or perhaps less than the time to reproduction of those species. The forcing for the change is generally external to the biological ecosystem, that is these changes are not simply biological oscillation patterns within the ecosystem, but arise from changes in the physical environment. This statement represents a mixture of observation and assumption for our discussion and analysis of regime shifts. Anthropogenic forcing can also represent an external forcing term, e.g., through restructuring the food web by fishing, as happened on Georges Bank in the 1950s and 1960s (Murawski & Idoine, 1992; Fogarty & Murawski, 1998) with the resulting shift from groundfish to elasmobranchs.

Synchrony between populations at the global (Chavez, Ryan, Lluch-Cota, & Niquen, 2003) or basin-scale (Hare & Mantua, 2000) is one of the supporting pieces of evidence that biological populations are being forced via density-independent factors. As pointed out by Moran (see Hudson & Catadori, 1999), biological populations can show synchronous changes, or oscillations, if they have the same density-dependent structure. Our understanding of the relative influence of density-dependent and density-independent factors is still limited, since we do not yet have convincing process models of what has led to the oceanic regime-shift examples that we discuss in this review. Dispersion may also play a role in synchronizing populations, an effect more likely to be important at shorter scales, and unlikely to play a role at the global scale (Sutcliffe, Thomas, & Moss, 1996).

Given that the time-scale of the states is decadal or longer, it might be expected that the spatial scale would also be large, perhaps coupled through the circulation field, but it is probably more appropriate to consider the spatial scale as defined by the population scale for the organisms involved. Such a definition allows us to determine if a shift is a result of changes within the scale of the community population or perhaps a result of geographic shifts along a population gradient, so called biogeographic shifts.

It is difficult to determine when the phrase 'regime shift' was first used, but our review of the literature suggests that the first use was by Isaacs (1976) (see Table 1). As the summary of relevant papers reveals, the concept of regime shifts remains fairly pliable and has been applied differently depending upon the ecosystem under study. The relationship between the observed changes in properties, and the ecosystem or ecosystem state, is generally not explored explicitly.

Many different types of change can take place or are observed in ecosystem variables. The movement from one state to another could be linear and rather gradual (Fig. 1a), and may not represent any substantial change in the dynamical ecosystem structure but rather represent a change in the ecosystem intensity. The smooth and linear curve also suggests that the changes are reversible, based upon the implied linearity of the response. The movement between states could also be rather abrupt in observation but still

Table 1
Marine science studies in which regime state or regime changes have been discussed, primarily from an observational perspective

Reference	Characteristics	Comments
Ideas and frustrations concerning fisheries science (Isaacs, 1976)	"Rather, there are probably a great number of possible regimes and abrupt discontinuities connecting them, flip-flops from one regime to another"	"Multifarious regimes involving biology or climate, or oceanography, or migrations, temperature, or weather, or combinations of these"
Russell Cycle in the English Channel (Southward, 1980)	".. sequence of changes in abundance and species of zooplankton and pelagic fish, accompanied by a fall in the winter maximum in inorganic nutrients"	Overriding influence of climate through biogeographic shift, direct changes of temperature and transport changes
Venrick, McGowan, Cayan, and Hayward (1987)	A long time series for Chlorophyll a in the central North Pacific showed concentrations nearly doubling between 1968 and 1985 in association with large scale changes in winter winds, surface pressures, and SSTs	Data were insufficient to determine whether changes in Chl a were continuous over time or a more rapid step-like change from one quasi-stable level to another.
World-wide sardine and anchovy fluctuations Lluch-Belda et al. (1989), Lluch-Belda et al. (1992)	"Of particular interest, in view of their impact on the world fish harvest and on national economies, are the prolonged "regimes" of high or low abundance of the species"	"The regime cycles are of two types. Type I includes sardines, while anchovies belong to type II. Each of the two types has its particular ecological characteristics and strategies"
Regime shifts in fisheries management (Steele, 1996)	Increasing evidence that there are concurrent changes in several stocks at these longer time scales. The term "regime shift" has been used to suggest that these changes are causally connected ..."	"The idea of regime shifts is not new. It is found in the work on the Russell cycle (Southward, 1980) and is implicit in "Climate and Fisheries" (Cushing, 1982). I do not know the ultimate origin of the term but first heard it used in a lecture by Warren Wooster"
Review of different oceanic environments: coastal, deep ocean and continental shelf (Steele, 1998)	Climatic changes at decadal scales produce or enhance regime shifts	"Phrase "regime shift" implies a coherent response, at the community level, to external stresses"
Climate-ocean variability in the Northeast Pacific (McGowan Cayan, & Dorman, 1998)	Documents increasing frequency of warm events in the past 20 years of the 80 year record	Changes in the physical environment act as disturbances on the ecosystem
North Pacific interdecadal variability (Miller & Schneider, 2002)	"A change from a persistent and relatively stable period of biological productivity that accompanies a change after a similarly stable period in physical oceanographic variables"	"Our presently imprecise understanding of the physical mechanisms of decadal variations and even greater obscurity of biological response mechanisms, makes it difficult to define "regime" precisely"
North Pacific integrated ecosystem index analysis (Mantua & Hare, 2002)	"There is no common definition of a regime shift, but certain aspects are generally agreed upon"	"A regime implies a characteristic behavior of a natural phenomenon over time" "A shift suggests an abrupt change in relation to the duration of a regime, from one characteristic behavior to another"
Catastrophic shifts in freshwater, terrestrial and marine ecosystems (Sheffer et al., 2001)	"conspicuous jumps from one rather stable state to another"	Observations are interpreted in connect of stability theory
Bering Sea pelagic ecosystem time series (Hunt & Stabeno, 2002)	Oscillating Control Hypothesis warm and cold regimes shift ecosystem from bottom up to top down control	Physical regime state changes lead to ecosystem oscillations
Global anchovy and sardine oscillations (Chavez et al., 2003)	Periods when 'sardines' or 'anchovies' are successful define the regime state	Based upon observations of 'cycles' or changes from one regime state to another

Table 1 (*continued*)

Reference	Characteristics	Comments
Regime shifts (Bakun, 2004, Chap. 25)	"persistent radical shift in typical levels of abundance or productivity of multiple important components of marine biological community structure, occurring at multiple trophic levels and on a geographical scale that is at least regional in extent"	
Benguela Current ecosystem (Cury & Shannon, 2004)	"A regime shift is considered to be a sudden shift in structure and functioning of a marine ecosystem, affecting several living components and resulting in an alternate steady state"	"Regime shifts differ from simple species replacement or alternation of species at similar trophic levels, whereby the ecosystem is not significantly altered in terms of its structure and function; only its species composition changes"
Regime shifts in the North Pacific (Wooster & Zhang, 2004)	"A regime shift can be defined as an abrupt change in a marine ecosystem and its abiotic environment from one stationary state to another."	
Methods for detecting regime shifts in large marine ecosystems (Mantua, 2004)	"*Regime shift*: a relatively brief time period in which key state variables of a system are transitioning between different quasi-stable attractors in phase space"	"*Regime*: a period of quasi-stable biotic or abiotic system behavior where temporal variations in key state variables are concentrated near distinct dynamical attractors, or stability wells, within phase space"

There is no consistent definition running through these papers nor a consistent approach to determining ecosystem state, or changes in the state, or the relation between the physical, chemical and biological environment that might determine the impulse for a change in regime.

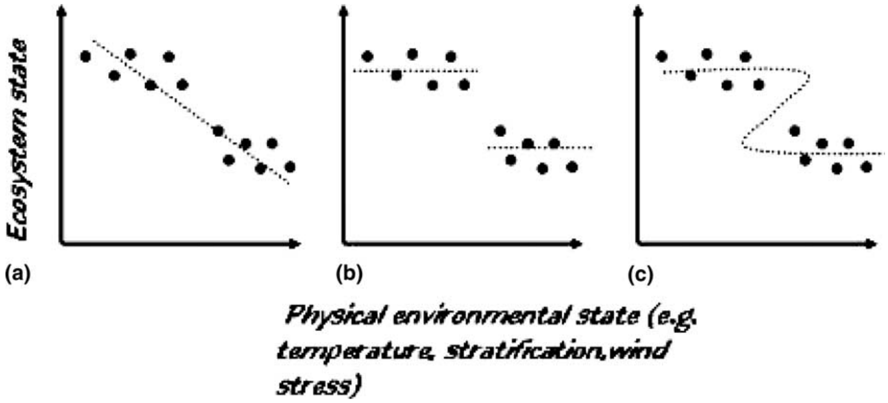

Fig. 1. Schema showing different possible interpretations of a common data set. The vertical axis is for the ecosystem state, perhaps normalized abundance for several different species, while the horizontal axis in time spanning many years, or perhaps physical environmental state, perhaps temperature. The dashed lines represent conceptual models of the data: (a) a linear evolution of declining overall abundance; (b) an abrupt but potentially reversible change in overall abundance; and (c) an abrupt change that is not directly reversible as the system exhibits non-functional response. In general these plots will be multi-dimensional as both ecosystem and physical state will require multiple variables for their definition.

linear in that it is directly reversible (Fig. 1b) or could be fully non-linear, rather abrupt and non-reversible (Fig. 1c). There are, therefore, three possible interpretations of this single artificial time-series depending upon the presumed errors associated with the data, other data available, known correlations of the data and conceptual models of the ecosystem function and state. While these plots, and in particular the now iconographic plot of Hare and Mantua (2000) for the North Pacific, can present much useful information and influence our thinking, they may also be misleading in that they of necessity collapse data, such as the geographic distribution, or in normalized form represent a scaling that is perhaps inappropriate.

We review examples from four different ecosystems to consider how data in each of these four different regions – the NE Pacific, the NW and NE Atlantic and Boundary (West and East) Current systems has been and could be used to determine if a regime shift has occurred. The data are limited, in that we have only a few measures of ecosystem state or function, and even where measurements do exist the signal to noise ratio, while unknown, is suspected to be quite small. These constraints make it difficult to provide definitive analysis of what has happened in each of these systems but bringing these case studies together does help us to understand whether our conceptual model, as illustrated in Fig. 1, is a useful guide to determining if regime shifts do take place in the ocean.

2. The North Pacific and analysing regime shifts

The stimulus for the identification of 'regime' structure is normally exploration of time-series and the appearance of hypothetical correlations (Polovina, Mitchum, Graham, Demartini, & Flint, 1994). On this basis the Pacific provides a reasonably well-documented case of 'regime' changes. A considerable body of literature has been devoted to the discussion of persistent widespread changes in Pacific basin climate (e.g., see Trenberth, 1990) and marine ecosystem properties, that took place in the late 1970s (Francis et al., 1998; Hare & Mantua, 2000). Recent reviews that have focused on both the physical and marine ecosystem aspects of 20th century Pacific Decadal Variability are provided by Mantua and Hare (2002) and Chavez et al. (2003). Key characteristics of the 1976/77 North Pacific and Bering Sea regime shift include:

- Basin scale (O(10,000 km)) environmental changes clearly expressed in atmospheric pressure fields, surface windstress, upper ocean temperatures and mixed layer properties, and Ekman transports in both the sub-arctic and northeast Pacific (Polovina et al., 1995; Miller et al., 2003).
- Relatively rapid shifts in phytoplankton and zooplankton production (Venrick et al., 1987; Brodeur & Ware, 1992), along with changes in zooplankton species assemblages in the California Current System (Peterson, Keister, & Feinberg, 2002).
- A shift from a highly productive benthic community of commercially valuable shrimp and crab populations to a similarly productive gadid population in much of the Bering Sea and Gulf of Alaska (Anderson & Piatt, 1999).
- A shift from very low to very high salmon production in Alaska coincident with a shift from relatively high to very low salmon production off California, Oregon and Washington (Hare, Mantua, & Francis, 1999).

The collection of physical and biological observations in the North Pacific provides compelling support for strong physical forcing of the marine ecosystems of the North Pacific and Bering Sea. In spite of the wealth of studies and observations, the mechanisms behind both the climate and ecosystem changes remain poorly understood. Even the degree of top-down versus bottom up forcing in the marine food-web is unknown.

Fig. 2 shows a typical set of variables for the North Pacific, here an atmospheric pressure index, water temperature and different biological measures that show low-frequency variability of phytoplankton, zooplankton and fish catch in the Northeast Pacific. The low-frequency character of these various time series is one source of our difficulty in using the data alone to define the regime shift, since a limited selection of the appropriate time-series would almost inevitably yield apparent correlations and also examples of regime changes. Indeed this well-known general problem of red-shifted (or highly auto-correlated) time

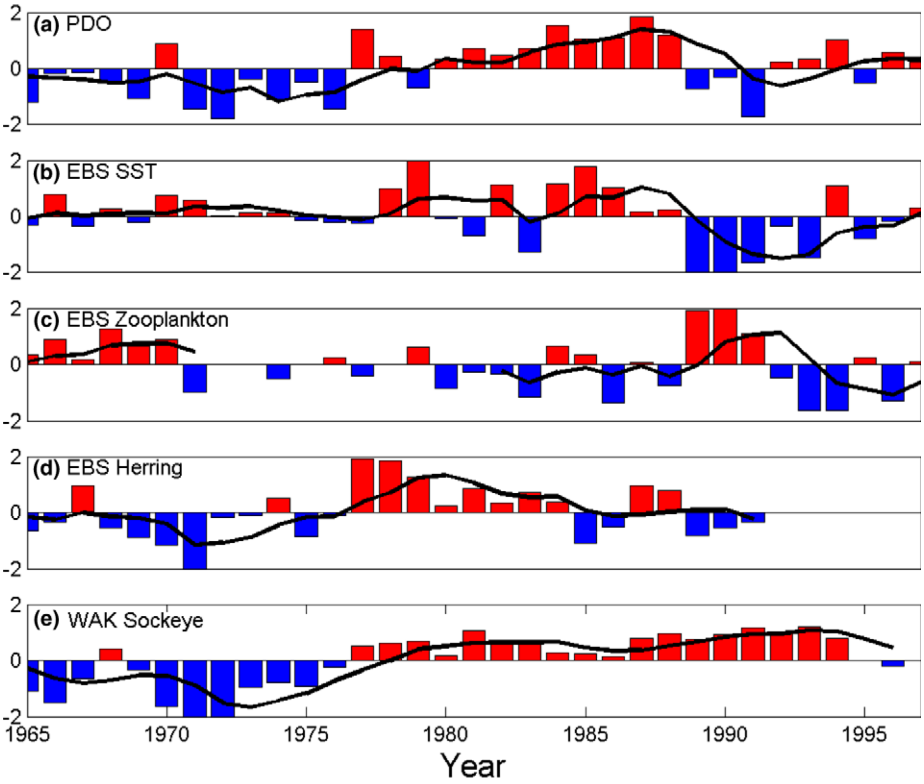

Fig. 2. Time series of (a) Pacific Decadal Oscillation; (b) sea surface temperature; (c) zooplankton; (d) herring abundance in the Eastern Bering Sea; and (e) catch of Western Alaska sockeye.

series has recently been explored in the context of regime-shift analysis by Rudnick and Davis (2003). Hare and Mantua (2000) assembled 69 biological and 31 physical time series for the Northeast Pacific and Bering Sea. Using principal components analysis, they identified 2 statistically significant patterns of variability, the first reproducing previously discussed aspects of the 1976/1977 North Pacific regime shift and the second pattern identifying temporally coherent changes around 1988/1989 in several Bering Sea species (e.g., chum salmon landings, jellyfish biomass, several groundfish stocks) as well several measures of salmon abundance and groundfish recruitment in the California Current. Following Ebbesmeyer et al. (1991), Hare and Mantua (2000) created a 100-member composite time series. This composite time series also suggested that regime shifts occurred in the North Pacific and Bering Sea around 1976 and 1988.

Rudnick and Davis (2003) demonstrate that with a random collection of Gaussian auto-correlated time series such a composite analysis will frequently produce step like changes, suggesting regime-like behavior when none is present. For example, using 100 random time series with the spectral properties of the PDO index, Rudnick and Davis found that the “composite regime test” is passed about 50% of the time. Hence they considered that the regime test based on the composite analysis is not reliable for detecting regime shifts.

It appears to be unlikely that any time-series analysis, independent of some process conceptual model or analysis, is ever likely to produce unequivocal proof of a regime change in such a complex system where the relationship between the different variables is so poorly understood. We ask the question, therefore, what

Table 2
Characteristics of different regime shifts can be summarized by defining the key characteristics of an oceanic regime shift

	NE Pacific	NW Atlantic	North Sea	Boundary Currents
Climate forcing	PDO	NAO/fishing	NAO/Regional warming	Teleconnections fishing
Spatial scale (km)	1000s	1000 (shelf)	1000 (50–60°N)	2–3000
Ecosystem restructuring	Phytoplankton, Zooplankton ≫ fish	Vertebrates ≫ Invertebrates	Zooplankton/fish community shifts	Zooplankton/fish community shifts
Time-scale of change (years)	1–5 years	5+ years	~5 years	?? years
Persistence time-scale (years)	20–30 years	10+ years	10+ years	10–40 years

The climate forcing signal is often identified as an atmospheric oscillation (e.g., the PDO, or the NAO) that drives variability in the ocean at similar time-scales. The spatial scale of the observed changes are in all cases very large although in some cases limited by the spatial scale of ecosystem, e.g., the shelves in the North Sea and the Northwest Atlantic. The time-scale for the change, and the persistence of the change, are often difficult to determine because of the weak signal-noise ratio and ambiguity in determining how appropriately to analyse the data (cf. Rudnick & Davis, 2003).

general understanding can we gain from the data themselves and from our present knowledge of ecosystem function in the Eastern and Western Boundary Currents, the Northeast and the Northwest Atlantic? These examples show how our table of general guidelines (Table 2) can assist in empirical determination of regime changes in the ocean.

3. Regime shifts in eastern and western boundary currents

Large anchovy (*Engraulis* sp.) and sardine (*Sardinops* sp.) populations live in the fertile upwelling ecosystems of eastern boundary currents (California, Humboldt and Benguela Current) and in the waters around Japan. They support important fisheries, mainly for fish meal production, and the economy of the riparian countries of upwelling systems depends on these fisheries (see: John Steinbeck's "*Cannery Row*"). The dynamics of these anchovy and sardine populations are characterised by their inverse relationships. When one species is doing well and supports a large biomass and high production, the other species usually sustains a rather low biomass (Lluch-Belda et al., 1989, Lluch-Belda et al., 1992; Schwartzlose et al., 1999, Alheit & Hagen, 2002). These shifts between sardine and anchovy-dominated states seem to restructure the entire ecosystem, as concomitant qualitative and quantitative changes in other ecosystem components have been observed. Because of their dramatic and long-lasting nature, these switches have been termed "regime shifts" (Lluch-Belda et al., 1989, 1992). The term *regime* was used by Isaacs (1976) to describe distinct climatic and/or ecosystem states and *regime shifts* are transitions between different regimes (Lluch-Belda et al., 1989, 1992; MacCall, 1996). Regimes in eastern and western boundary current systems generally persist for between 10 and 40 years. Dominance of particular small pelagic fish species in the northern and southern Benguela ecosystems have been sustained over periods of 10–30 years, and changes in the Peruvian ecosystem have occurred on time-scales of 15–30 years. Model simulations of ecosystem changes in the southern Benguela suggest that environmental perturbations affecting zooplankton over three-year and 10-year periods may cause ecosystem changes over 10 and 20 years, respectively (Shannon, 2001; Shannon, Field, & Moloney, 2003).

Most data on fish population dynamics stem from the fisheries. Catch data are a somewhat crude measure of fish abundance; however, they usually give an acceptable indication of trends in population dynamics. The geographical distributions of anchovies and sardines in particular depend very much upon stock size and migratory behaviour (Schwartzlose et al., 1999). During periods of high biomass, sardines expand rapidly poleward, shifting their main spawning and feeding areas (Lluch-Belda et al., 1992). The geographical extensions given here refer to the combined extreme ranges of both genera.

Humboldt Current. Perhaps the best example of alternating anchovy and sardine periods has been observed in the Humboldt Current (Alheit & Bernal, 1993; Alheit & Niquen, 2004), which is inhabited by eight discrete clupeoid stocks (three *Engraulis* stocks, four *Sardinops* stocks, one *Strangomera bentinki* stock). Their combined area of distribution reaches from 1°S off southern Ecuador in the North to about 42° S off central Chile. The most northerly stocks are separated by thousands of miles from those in the south. In spite of the large distances, they all exhibited similar dynamics with high/low biomass in the 1960s until about 1970, then reversing to low/high biomass until the second half of the 1980s and returning thereafter again to high/low biomass as in the 1960s. It was in 1970 when the Peruvian anchovy, once the world's largest single-species fishery, crashed from a peak of 12.5 million MT to an average catch below 3 million MT throughout most of the 1970s. The shift from an anchovy to a sardine regime in the Humboldt Current in the late 1960s was accompanied by dramatic decreases in zooplankton biomass as demonstrated by two independent zooplankton time series collected off Peru (Carrasco & Lozano, 1989) and northern Chile (Bernal, Robles, & Rojas, 1983). Also, Loeb and Rojas (1988) observed a marked shift in the relative abundance of the early larvae of the nonfished mesopelagic species from 1969 to 1970. Recently, it has been shown by analysing accumulation rates of fish scales in anoxic sediments that there was a sardine period in the 1930s and 1940s in the Humboldt Current (Baumgartner, pers. comm.; Schwartzlose et al., 1999, McFarlane, Smith, Baumgartner, & Hunter, 2002).

California Current. In the California Current, the distribution of sardines and anchovies ranges from southern Alaska (57°N) to the southern tip of Baja California (23°N) (McFarlane et al., 2002). Both species also inhabit the Gulf of California. The California sardine fishery peaked in the mid-1930s, collapsed in the 1950s and the stock was considered almost extinct in the 1970s. There was evidence of a recovery in the early 1980s and the catches increased noticeably in the 1990s (Fig. 3). The central stock of the Californian anchovy showed peak catches from the mid-1970s to the early 1980s. The fishery declined sharply in the 1990s and has remained at low levels since. Its biomass peaked from 1973 to 1976 (Schwartzlose et al., 1999). A strong sardine regime in the California Current was observed from the early 1930s with high catches in the 1930s and 1940s. This then gave way to an anchovy regime from the early 1970s to the late 1980s/early 1990s. Another sardine regime seems to have been established since then. The sardine fishery in the Gulf of California began in the late 1960s, as the sardine fishery of the west coast of Baja California declined. Catches peaked in the late 1980s, then declined dramatically and increased again in the mid-1990s (Schwartzlose et al., 1999). Biomass estimates of the adult population from virtual population analysis showed an increase of the stock from 1975, a peak in 1985/1986 and a subsequent decrease. The level of recruitment showed a similar pattern (Schwartzlose et al., 1999). This seems to indicate a sardine regime from the mid-1970s to the late 1980s.

Japanese waters. There are two subpopulations of the Japanese sardine (Schwartzlose et al., 1999). One is distributed in the Sea of Japan and the East China Sea. The second ranges along the Pacific coast of Japan. A sardine period was recorded from the 1920s to the 1950s. These catches were mainly from the Sea of Japan. Beginning in 1950, anchovy catches increased considerably, maintained high values from 1955 to 1970, and then declined to rather low levels until 1990 when catches increased again. Sardine catches started to increase again in 1971, rose dramatically from the mid-1970s to peaks in the 1980s and then declined continuously from 1989 to the present. Catches during this sardine regime were mainly from the Pacific subpopulation. As in the Humboldt Current, zooplankton biomass was much higher during the anchovy period.

Benguela Current. In the Benguela, regime shifts occur along coastlines of around 1600 km (northern Benguela, off Namibia) to 2000 km (southern Benguela, south of the Luderitz Upwelling Cell), affecting areas around 180,000 and 220,000 km^2, respectively, in the northern and southern Benguela systems. Off

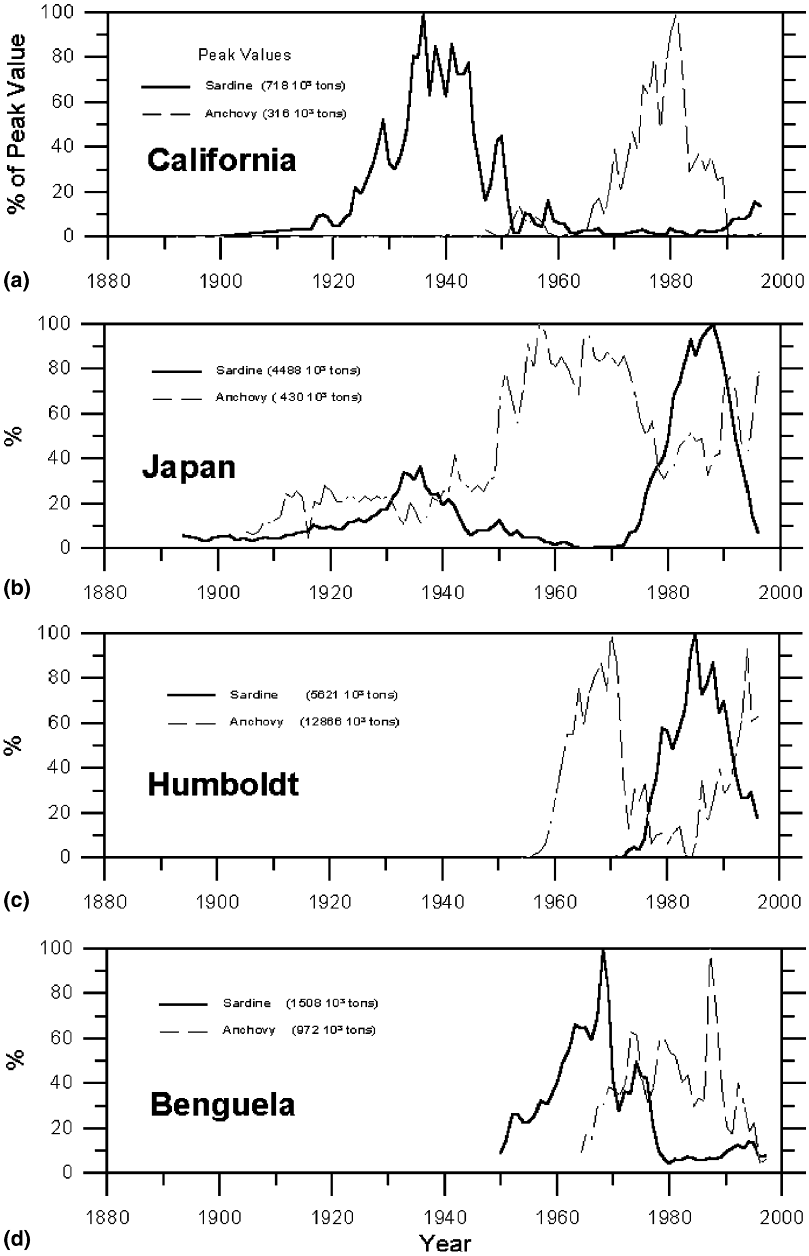

Fig. 3. Variation in the annual catch of sardine and anchovy in four major current systems during the 20th century. Variations in fish catches plotted as percentages of maximum historical annual values.

South Africa, anchovy *Engraulis capensis* were abundant in the 1920s, declined in the early 1930s (Crawford & Jahncke, 1999) and remained low until the 1960s. Horse mackerel *Trachurus trachurus capensis* dominated the southern Benguela ecosystem during the 1940s and early 1950s. Fairly stable catches of sardine *Sardinops sagax* were made in the 1950s, but underwent a large decrease in the early 1960s. Subsequently, and with the introduction of smaller meshed nets, anchovy were then targeted by the fishery from the mid-1960s onwards. Sardine biomass declined steadily, reaching very low levels by the early 1980s. During the later part of the 1980s and the 1990s, there were large fluctuations in anchovy biomass, and sardine began to increase, such that both anchovy and sardine were present at high abundances in the late 1990s and early 2000s. As in the south, sardines were abundant in the northern Benguela system (off Namibia) in the 1960s, but subsequently declined. Thereafter, the sequence of pelagic fish fluctuations in the northern Benguela differed from that in the southern system. There was no clear shift from a sardine to an anchovy regime, but rather, a suite of planktivorous fish took sardine's place in the late 1970s and early 1980s: horse mackerel (*Trachurus capensis*), bearded goby (*Sufflogobius bibarbatus*) and also anchovy (*E. capensis*, Boyer & Hampton, 2001). Between 1986 and 1991, sardine and hake abundances increased, but by the late 1990s, biomass of most fish stocks was low (Boyer & Kreiner, in press).

Ecosystem restructuring has been observed during regime shifts in the Benguela. For example, in the northern Benguela there has been a shift from a sardine-dominated system in the 1950s and early 1960s, to a system that is now dominated by jellyfish, pelagic goby and horse mackerel (although horse mackerel have declined in recent years in conjunction with large declines in most fish stocks in the northern Benguela). Seals and seabirds preying on small pelagic fish off Namibia have been severely affected. For example, gannets breeding off Namibia have undergone a longterm, dramatic decline, corresponding to the decrease in sardine abundance (Crawford, 1999). In the southern Benguela, there have been changes in zooplankton community structure between the 1950s, when sardine was dominant, and the 1990s, when anchovy fluctuated (after a period of dominance in the 1980s) and sardine was again on the increase (Verheye & Richardson, 1998).

As has already been recognised, regime shifts seem to happen synchronously all over the Pacific Ocean (Lluch-Belda et al., 1989, 1992). Fluctuations in populations of anchovy and sardine off Japan, California and South America (Humboldt Current system) are well matched and appear to be influenced by global-scale environmental forcing (Kawasaki, 1983; Crawford et al., 1991, see Fig. 3). Thus, the sardine populations off Japan, in the Humboldt and in the California Current supported high biomasses during the 1930s and the 1940s. These stocks decreased dramatically during the 1950s and 1960s, rose again in the 1970s and 1980s (except California Current sardine) and biomass decreased since the late 1980s (Schwartzlose et al., 1999; Alheit & Hagen, 2001, 2002). Interestingly, North Pacific salmon populations exhibited the same population swings. Further, Alheit and Hagen (1997) showed that in the eastern Skagerrak, English Channel and Bay of Biscay, alternation between periods dominated by herring and sardine seem to be governed by the same climatic variations as those driving the Pacific upwelling regions. By comparison, small pelagic fish fluctuations in the Benguela and Canary current systems are out of phase with the Pacific ecosystems (Lluch-Belda et al., 1989, Schwartzlose et al., 1999). The sardine stocks in the Benguela Current showed population fluctuations and were at their maximum biomass when the Pacific sardines were at low population levels. In contrast, anchovy populations in the Humboldt Current and in Japanese waters were thriving in the 1950s and 1960s, declined around 1970 and started to increase again in the second half of the 1980s. However, the California Current seems to have been out of phase with the other regions since the 1950s. The Californian anchovy population started to rise in the early 1970s, peaked in the 1980s and declined again in the late 1980s, showing a pattern of population dynamics very similar to that of the Japanese and Humboldt sardines. In contrast, the Californian sardine started to rise in the late 1980s, just as the landings of Japanese and the Humboldt anchovies began to increase.

The process of replacement of one species by another during a regime shift may be strongly influenced by fishing (Crawford, Shannon, & Pollock, 1987). For example, in the northern Benguela, sardine abundance began to decline towards the end of the 1960s, cause for concern as sardine is commercially more valuable than anchovy. In an attempt to favour sardine above anchovy by alleviating competition between anchovy and sardine, anchovy was heavily fished in the 1970s (Butterworth, 1983). The outcome was that both stocks collapsed off Namibia, the vacant niche being filled by a suite of species: horse mackerel, pelagic goby and jellyfish (Boyer & Hampton, 2001).

Regime shifts in eastern and western boundary current systems are sometimes relatively abrupt, such as in the Humboldt system discussed above. However, ecosystem changes in these productive systems may also be more gradual, such as the decrease in sardine and increase in anchovy in the southern Benguela ecosystem in the late 1960s and 1970s, which appeared to have had gradual effects on other ecosystem components as well.

Whether regime shifts in boundary current systems may be reversible is uncertain. Reversibility has been observed in the past. For example, in the southern Benguela, sardine, which were the dominant small pelagic fish in the 1950s, declined to very low levels in the 1970s and 1980s but have recovered to high biomass levels again in the recent decade. In the case of top-down induced regime shifts (such as through heavy fishing pressure), ecosystem changes may at least be long-lived, if not permanent. In the northern Benguela ecosystem, it has been suggested that environmental perturbations, exacerbated by heavy fishing, have resulted in many fish stocks reaching dangerously low levels in recent years (Boyer & Hampton, 2001). Whether the system is now "trapped" in this low biomass state or whether it may still recover is not known. Mechanisms that may sustain the system at this low biomass state have been considered (e.g., Boyer, Boyer, Fossen, & Kreiner, 2001), and it has been proposed by Cury and Shannon (2004) that fishing may sensitize an ecosystem to environmental effects, i.e., bottom-up regime shift forcing may be stronger in such a system.

4. The Northeast Atlantic

In the North Sea the term regime shift has been used to describe large decadal scale switches in the abundance and composition of plankton and fish (Reid, Borges, & Svenden, 2001a). As has already been described such an event took place in the central gyre of the Pacific Ocean during the mid-1970s. Venrick et al. (1987) reported increases in phytoplankton biomass, which they attributed to modification of atmospheric circulation. The reinforced sea level pressure increased the strength and frequency of storminess and west winds which allowed a deeper mixing and more nutrients to be brought to the surface. Brodeur and Ware (1992) found changes in zooplankton biomass in the Central Subarctic Pacific. Changes in Ekman pumping in the gyre is proposed to have modified the carrying capacity of the central North Pacific gyre, contributing to an increase in the abundance of fish such as the Alaskan salmon and cod and a decrease in the abundance of shrimps (Botsford, Castilla, & Peterson, 1997).

It has been suggested that a similar regime shift also occurred in the North Sea after 1988 (Reid et al., 2001a). This involved an increase in phytoplankton biomass (Reid, Edwards, Hunt, & Warner, 1998), a change in plankton community structure and phenology (Reid et al., 2001a) and was also detected in the benthos. Many changes in the biological composition of North Sea marine ecosystems were also observed at the end of the 1980s (e.g., Lindley et al., 1990; Lindley, Williams, & Hunt, 1993; Greve, 1994). This cascade of biological events was accompanied by an increase in catches of horse mackerel (Reid et al., 2001a) and changes in benthic community structure in the southern North Sea (Kroncke, Dippner, Heyen, & Zeiss, 1998). Physical–chemical changes, such as an increase in sea surface temperature and changes in the concentration of certain nutrients and oxygen, were also detected in the Skagerrak at about the same time (Dahl & Danielssen, 1992; Reid et al., 2001a). Recently, Beaugrand and Ibañez (2002) showed that the regime shift also involved an increase in calanoid copepod diversity. The main calanoid copepod assemblages in the North Sea showed a pronounced change during the 1980s (Figs. 4(a)–(c)). This reorganisation in community structure resulted in an increase in the total diversity of this group (Fig. 4d) and paralleled a stepwise increase in Northern Hemisphere Temperature anomalies.

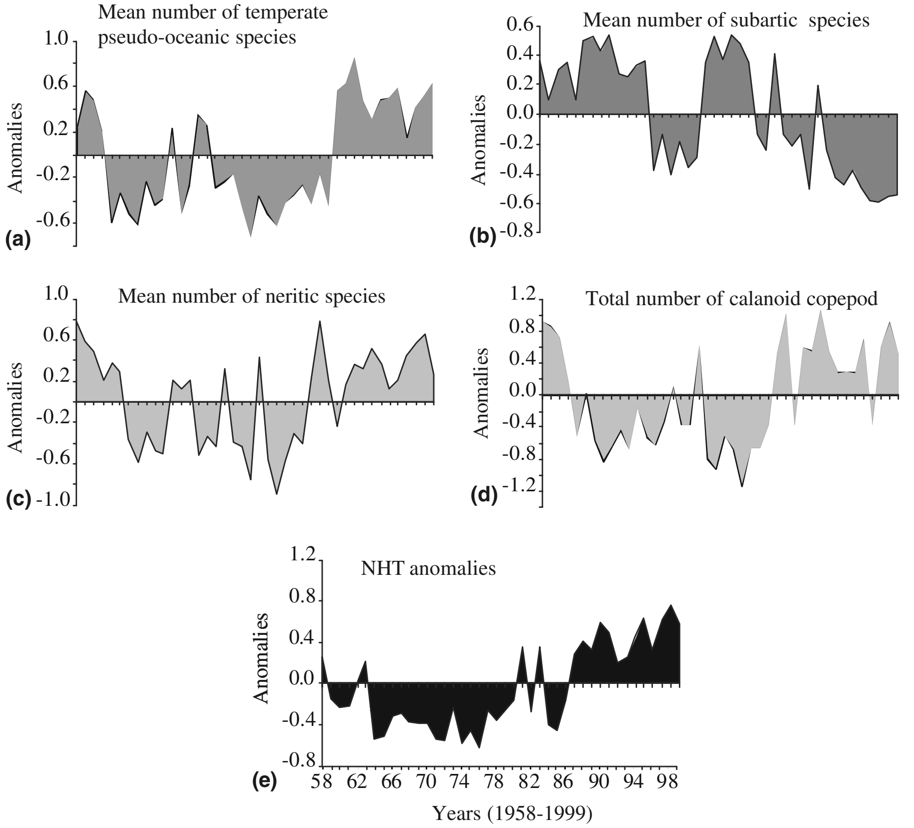

Fig. 4. Long-term changes in calanoid copepod community structure in the North Sea. Species assemblages used in this figure are those used in Beaugrand, Reid, Ibañez, Lindley, and Edwards (2002). Data are from Beaugrand (2004a). Data were standardized and transformed using a square root function to minimize the effect of episodic or exceptional events. (a) Mean number of temperate pseudo-oceanic species per CPR sample. (b) Mean number of subarctic species per CPR sample. (c) Mean number of neritic species per CPR sample. (d) Mean number of calanoid copepods per CPR sample (used as an index of diversity). (e) Northern Hemisphere Temperature (NHT) anomalies. The shadow bar emphasizes the period of pronounced change.

To date, the origin of the regime shift in the North Sea still remains unclear. Holliday and Reid (2001) and Reid, Holliday, and Smyth (2001b) have recently provided evidence that the European Shelf-Edge Current may play an important role. Holliday and Reid (2001) investigated the transport of oceanic water into the Rockall Trough. They found that the mean volume transport reached about 7 Sv in 1989 and 1998, nearly twice the usual 3.7 Sv. These two events coincided with two episodic oceanographic events during the late 1980s (Edwards, Reid, & Planque, 2001) and the late 1990s (Edwards, John, Hunt, & Lindley, 1999). The latter event was not clearly detected in the diversity and community structure of calanoid copepods. Subsequently, Reid et al. (2001b) provided evidence that strong northward advection of warm water along the European shelf edge coincided with these two pulses of oceanic inflow into the North Sea.

Beaugrand, 2004b provides further analysis of the nature of the regime shift in the North Sea. This regime shift probably reflects a major reorganisation in the structure and composition of marine ecosystems observed in the North-East Atlantic since the beginning of the 1980s (Beaugrand et al., 2002). Along the European shelf-edge, a poleward movement of warm-water species has been detected, associated with a decrease in the mean number of colder-water species. All these biological changes, correlated with the increased sea surface temperature in the north-east Atlantic, are thought to reflect an ecosystem change

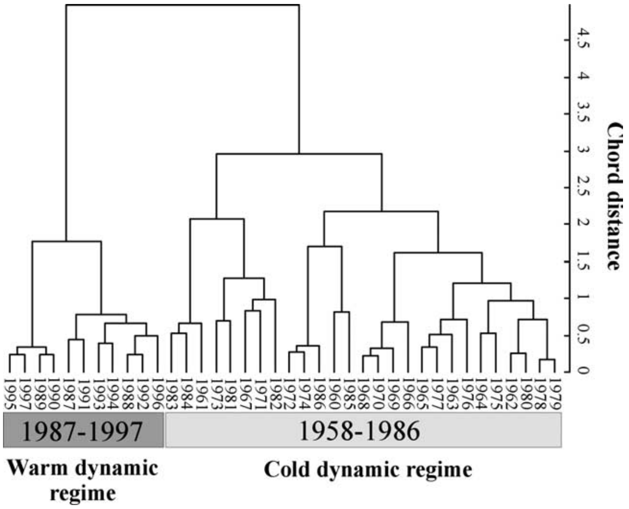

Fig. 5. Dendrogram of a cluster analysis performed on both physical and biological variables in the north-east Atlantic and the North Sea for the period 1960–1997. Two periods are distinguished: 1960–1986 (cold dynamic regime) and 1987–1997 (warm dynamic regime). Physical variables: sea surface temperature, North Atlantic Oscillation index, Northern Hemisphere Temperature anomalies. Biological variables: phytoplankton colour, total number of copepods, abundance of *C. finmarchicus*, abundance of Euphausiids and abundance of the Atlantic salmon *Salmo salar*. Modified. From Beaugrand and Reid (2003).

towards a warmer dynamical equilibrium. This large-scale reorganisation has probably played a key role in the North Sea ecosystem changes but is not the only factor. Beaugrand (2003) has shown that there was a stepwise decrease in the abundance of *Calanus finmarchicus* after the mid-1980s which corresponded with a stepwise increase in the value of the North Atlantic Oscillation and regional hydro-climatic variables such as temperature and wind stress. Based on changes at three trophic levels and changes in key hydro-climatic parameters (Fig. 5), the period 1987–1999 was identified as being exceptional in a 42-year record (Beaugrand & Reid, 2003). Reid, Edwards, Beaugrand, Skogen, and Stevens (2003) have suggested that the prolonged period of positive NAO may have favoured oceanic inflow into the North Sea and influenced the long-term changes of the dominant species *C. finmarchicus*.

5. The Northwest Atlantic

The application of industrial fishing to Georges Bank led to changes in the fish community structure that have persisted for more than 40 years (Fogarty & Murawski, 1998). There was a replacement of groundfish, cod, haddock, and flounder, by primarily elasmobranchs, dogfish, skate and mackerel. As noted by Steele (1998) such dramatic changes in community composition are not as catastrophic in marine ecosystems as comparable terrestrial human interventions, e.g., clear-cut logging. Indeed, it is not even clear that there is a substantial change in overall fish biomass despite the dramatic change in fish species structure. Steele (1998) refers to such changes as examples of "fungibility" in marine ecosystems, that functional group replacement is possible. Although it is clear that fishing removed the groundfish, it is not understood why the elasmobranchs increased in abundance and why, following the removal of fishing pressure, the groundfish did not return. One possible hypothesis is that elasmobranchs removed groundfish through predation, however, stomach analysis of elasmobranchs does not support this (Link, Garrison, & Almeida, 2002). It has been suggested that the elasmobranchs increased in abundance because of competitive release as groundfish abundance declined (Fogarty & Murawski, 1998). Competition between species may also play a role in hindering the recovery of the groundfish stocks in the presence of the more abundant elasmobranchs (Murawski & Idoine, 1992).

Farther north, along the continental shelf of the Northwest Atlantic of eastern Canada, there have been similarly dramatic changes of fish and species abundance over the past few decades. While it is clear that most of the decline in groundfish abundance is a result of overfishing (Hutchings & Myers, 1994), there is also evidence that environment played a role in the decline by influencing such things as distribution and recruitment (deYoung & Rose, 1992) and weight-at-age (Rose, deYoung, Kulka, Goddard, & Fletcher, 2000), an important component of overall productivity. There is a strong relation between temperature and general growth of cod across the North Atlantic (Brander, 1995), and evidence for a relationship between cod recruitment and temperature in the Northeast (Sundby, 2000) and Northwest Atlantic (deYoung & Rose, 1992; Rose et al., 2000). The process that regulates this influence of temperature on recruitment is not known. Analysis of fish assemblages on the Grand Banks (Gomes, Haedrich, & Villagarcia, 1995; Casey, 2000) provides some evidence that even those fish not directly harvested declined in synchrony with the over-fished species such as cod and haddock. For example, species such as American plaice (*Hippoglossoides platessoides)* also declined even though subject to much lower levels of exploitation (Bowering, Morgan, & Brodie, 1997).

While the collapse of the groundfish stocks in the Northwest Atlantic has received much attention in both the scientific (Hutchings & Myers, 1994) and the popular literature (Kurlansky, 1997), the shift from teleost groundfish to invertebrates, primarily snow crab (*Chionoecetes opilio*) and shrimp (*Pandalus borealis*) has only just begun to receive much scientific attention (Parsons & Lear, 2001; Worms & Myers, 2003). There has been a substantial shift in fishing effort, arguably accounting for the changes in the relative catch (see Fig. 6), but there has also been a rather abrupt shift in relative abundance. From the early 1950s until the late 1980s abundance of groundfish has declined in the Northwest Atlantic, punctuated by a few brief periods of recovery (e.g., in the early 1980s). The external forcing in this ecosystem, as noted above, primarily harvesting of fish by humans, has been fairly persistent over the past 50 years. It does appear, however, that the ecosystem response has been quite dramatic and extends beyond groundfish. As shown by Hutchings (2000), the recovery of fish stocks that have undergone a substantial decline in abundance generally takes decades or longer, but in the case of the Northwest Atlantic the surprise is not the slow recovery but the near absence of any signs of recovery.

The changes in the Northwest Atlantic ecosystem have also taken place at lower trophic levels (Greene & Pershing, 2000; Sameoto, 2001). Sometime between the late 1980s and the early 1990s, based upon the greenness index of the Continuous Plankton Recorder, there has been a dramatic change in phytoplankton biomass, with an increase in fall production, primarily dinoflagellates (see Fig. 6e).

Substantial changes in phytoplankton biomass, and shifts in zooplankton distribution, have also been observed in the Northeast Atlantic with evidence for an increasing trend in phytoplankton abundance that is associated with climate forcing in the North Atlantic (Edwards et al., 2001; Beaugrand & Reid, 2003) during this same period. There have been some changes in zooplankton on the Scotian Shelf with a shift around 1991 in the concentrations of key species, *C. finmarchicus* and *Paracalanus–Pseudocalanus* (Sameoto, 2001). The dominant physical environmental signal over the past 40 years in the Northwest Atlantic has been the North Atlantic Oscillation (NAO) (Fig. 6g) whose index is determined by taking the pressure difference between the Azores and Iceland (cf. Marshall et al., 2001) or some similar pair of stations which span the Atlantic from south to north. While the overall spectrum of the NAO, over the past 100 years, is very close to white noise (Greatbatch, 2002), the index has shown substantial decadal periodicity over the past 50 years. During this period NAO variability has been strongly correlated with many other environmental variables (including sea surface temperature, air temperature, rainfall, etc.) in both the Northeast and Northwest Atlantic.

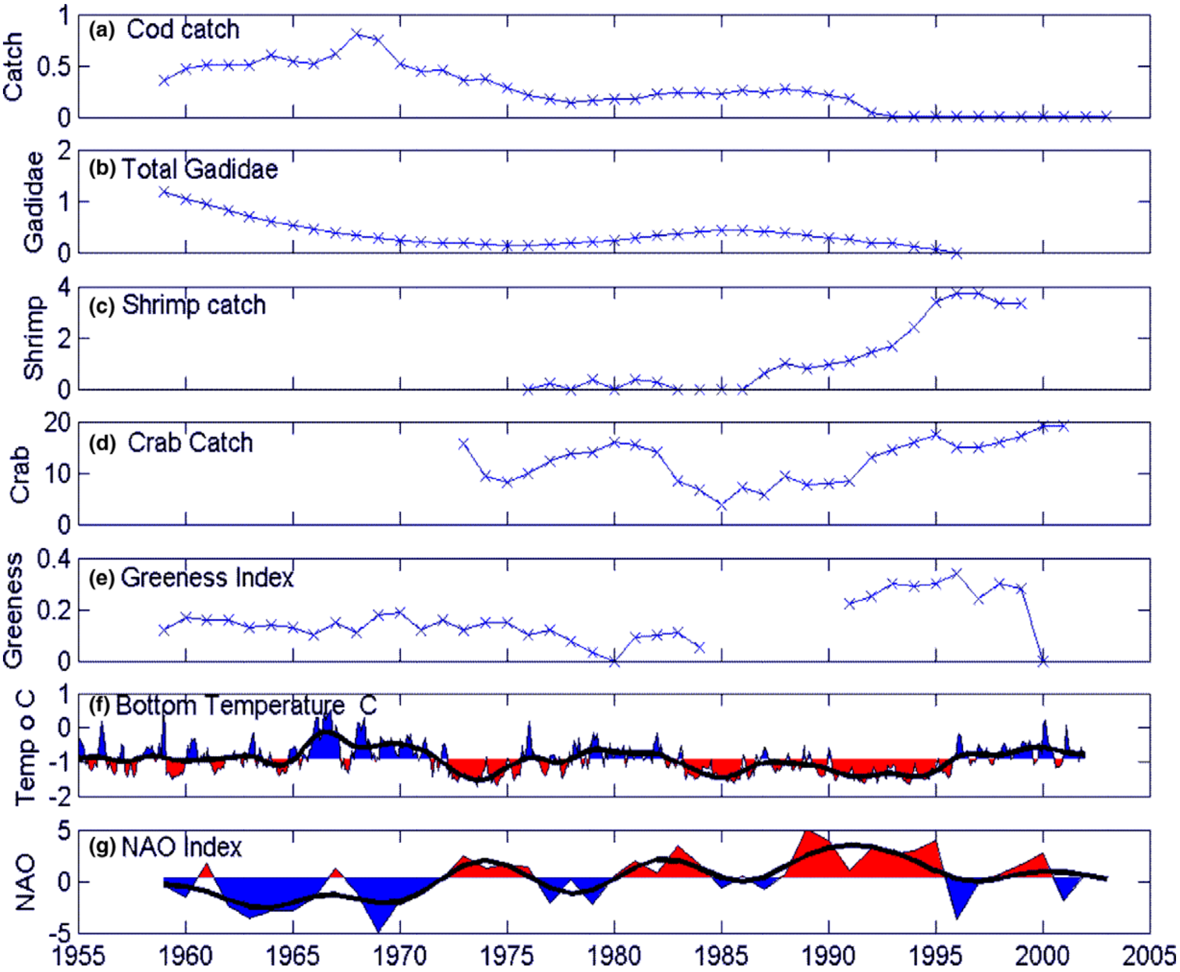

Fig. 6. Time series of (a) catch of cod (in 10^6 tonnes) over the Newfoundland and Labrador shelf (b) the total abundance of Gadidae over the southern Newfoundland shelf (c) the catch of shrimp and (d) crab over the Newfoundland and Labrador shelf (e) the greenness index from the Continuous Plankton Recorder (CPR) over the southern Newfoundland Shelf (f) bottom temperature from inshore on the southern Newfoundland shelf and (g) the North Atlantic Oscillation (NAO) index. The heavy solid lines in panels (f) and (g) represent low-pass filtered smoothed curves of the plotted data.

At higher trophic levels abundance of groundfish and invertebrates has also changed (see Fig. 6) over much of the Northwest Atlantic continental shelf (Drinkwater, 2002). Worms and Myers (2003) analysed the data for shrimp and cod over the past 25 years and have discovered a clear top-down predatory effect. The predator–prey relation between cod and shrimp extends back to before the collapse of the groundfish, but the dramatic increase in shrimp abundance is now clearly related to the decline of the groundfish. Similar analysis has been carried out with crab and the groundfish with broadly similar results (Myers, personal communication). Shrimp biomass was not related to temperature but that of cod was positively related to temperature. Worms and Myers (2003) conclude that these changes in relative abundance do not correspond to a regime shift in the sense of Hare and Mantua (2000) and Anderson and Piatt (1999), because the primary causal connection is between the cod and shrimp and not external climate forcing.

During this same period, the early 1990s, there were also substantial changes in seabird abundance and diet (Carscadden, Montevecchi, Davoren, & Nakashima, 2002; Montevecchi, Cairns, & Myers, 2002; Montevecchi & Myers, 1997). The breeding success of black-legged kittiwakes declined during the early 1990s, primarily because of changes in the migration timing and distribution of capelin (Carscadden et al., 2002) their primary prey during the breeding season. Gannet diets revealed shifts towards cold water species. Most of the changes in capelin timing and distribution and seabird breeding, which occurred during the early 1990s in response to below-normal sea temperature, have persisted even though temperatures returned to normal during the late 1990s (Fig. 6). Beginning in the late 1980s, capelin growth has slowed, and there has been delayed spawning with a southward shift in distribution (Frank, Carscadden, & Simon, 1996), with most of these changes attributed to cooler waters in the early 1990s (Carscadden, Frank, & Leggett, 2001). There have also been dramatic changes in pup-production of harp seals in the Northwest Atlantic during this same period. Production declined during the early 1960s reaching a low sometime during the early to mid 1970s, but since 1980 production has almost doubled (Stenson et al., 2002). It has been suggested that two reasons for the failed recovery of the groundfish stocks are the increase in seal abundance and that seals spend more time in Newfoundland waters. Predation would lead to increased mortality, apparently the primary factor limiting the present recovery of the groundfish stocks (Rice, 2002).

Although the observed changes in the Northwest Atlantic do meet the key criteria that we have defined for a regime shift, our understanding of what has taken place in this ecosystem is still limited. The spatial scale for the changes is much of the Newfoundland and Labrador shelf, one of the largest shelf systems in the world, so clearly the spatial scale is very large (O 1000 km). There have been changes in climate forcing during this period, with the cooling of water being the largest signal, although there have also been decadal oscillations as well as a trend to the climate forcing. A substantial restructuring of the ecosystem certainly has taken place at the upper trophic levels, with a shift from an ecosystem dominated by vertebrate groundfish to one in which invertebrates, crab and shrimp, play a much larger role. While the change has not been sudden, i.e., within a year or less, it has been short relative to the persistence time-scale of the populations, which appears to be at least many decades. It may well be that many, but not all, of the ecosystem changes are a result of human intervention. Certainly the removal of fish from this ecosystem over the past 50 years has played an important, and perhaps the dominant role in this region. Yet fishing has been an important factor in all coastal ecosystems over the past 50 years, as our ability to hunt and catch fish has improved, and it may well be that many of the observed changes in marine ecosystems are in some manner related to the effects of fishing and overfishing.

6. Conclusions

The operational concept of regime shift developed here is testable against data, as is shown in the review presented, but does perhaps leave open the question of the dynamical process changes occurring in marine ecosystems. For practical purposes, it is probably useful to accept as a regime shift changes in marine system function that are relatively abrupt, persistent, occurring at large spatial scales, observed at different trophic levels and related to climate forcing. Such regime shifts may not have the clear non-linear dynamical character that has been observed in terrestrial and freshwater systems (Sheffer et al., 2001) even though the phenomenological time series may exhibit broadly similar behaviour. The difficulty in experimental testing within the ocean, with the notable exception of iron fertilization experiments (Coale, 1996) and some large-scale mesocosm experiments (Harris et al., 1982; Reeve, Grice, & Harris, 1982), limits our ability to determine the reversibility of many of the changes that have been observed over the past one hundred years. There is also some uncertainty as to how many different stable states there really are, an issue connected to the problem of understanding what we really mean by an ecosystem and how 'fungible' the different structural components of these systems truly are (Steele, 1998). We suggest that applying an operational definition of regime shifts, and working to define regime structure and dynamics, will help us to understand marine ecosystems better.

The ecosystems that we have reviewed all exhibit substantial changes in ecosystem status and function. We have used the observed changes to determine whether the observed changes help us to define and understand ecosystem state and shifts in state. The characteristics that we have discussed include:

1. Global synchrony in small pelagics from boundary current systems in Japan, California, the Humbolt and Benguela with various phasings but interdecadal "regimes".
2. Regional scale climatically induced regime shifts in the NE Atlantic and North Sea marine ecosystems, apparently partly driven by range shifts related to upper ocean warming and ocean advection.
3. Strong top-down fishing impacts in the NW Atlantic and Georges Bank with a potential role for climate, yet only modest correlations between climate changes and ecosystem changes.
4. Very large-scale (1000–10,000 km) changes in the physical environment coherent with top to bottom changes in North Pacific and Bering Sea marine food webs.
5. Some evidence for range shifts in small pelagics and some zooplankton species in the California Current System, but also major shifts in community structure that aren't simply reflecting geographic shifts (e.g., from shrimp and crab to cod and Pollock in the Gulf of Alaska and Bering Sea; North-South inverse production pattern in Pacific salmon).

Should we expect regime shifts to become more likely in ecosystems than in the climate system? As noted in the introduction, "climatic regimes" appear to exist at millennial and longer time-scales, but at sub-millenial time-scales all the evidence seems to point to the kind of Gaussian red-noise that is discussed in the analysis of Rudnick and Davis (2003). Can we even distinguish the Gaussian red-noise in the environment from more regime-like changes in marine ecosystems? While it has been possible to separate these signals in at least some freshwater systems (cf. Sheffer et al., 2001), so far it has proven to be much more difficult in marine ecosystems. At present, we may have to be satisfied with a broader, and perhaps less ecologically precise, definition of regime shift in marine ecosystems.

Acknowledgements

The authors thank Louis Legendre and John Steele, organizers of the Symposium on Regime Shifts in the Ocean, who brought us to together to discuss this interesting and challenging problem. We also acknowledge the other participants at the symposium whose ideas and presentations stimulated our thinking.

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